

# THE UPPER CARBONIFEROUS TETRAPOD ASSEMBLAGE FROM NEWSHAM, NORTHUMBERLAND

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**ABSTRACT.** The Upper Carboniferous amphibians from Newsham in Northumberland constitute one of only five large, compact tetrapod assemblages known from the Westphalian of Europe and North America. The environment in which the Newsham tetrapods were preserved appears to have been a large and deep freshwater lake occupying a stretch of abandoned river channel. The lake was apparently surrounded by swamp-forest dominated by arborescent lycopods; sphenopsids, including *Calamites*, probably grew around its shoreline.

A revised list of the (eight) Newsham tetrapods which are certainly determinate at least to family level is presented. Specimens probably representing three additional species, including a colosteid temnospondyl, are described. A census of tetrapod specimens from the site facilitates distinction of the abundant endemic species from those representing erratics from environments other than that in which they were preserved. The eogyrinid embolomere *Eogyrinus attheyi* Watson, the loxommatid *Megalocephalus pachycephalus* (Barkas) and the keraterpetontid nectridean *Batrachiderpeton reticulatum* (Hancock & Atthey) seem to have been endemic in life to the Newsham lake. The aïstopod *Ophiderpeton nanum* Hancock and Atthey, a lysorophid and a urocordylid nectridean are each represented by only a single specimen and are regarded as possible erratics from water bodies smaller and shallower than the Newsham lake. The colosteid specimen is probably also derived from a shallow-water/swamp-lake environment, as may be the material representative of the medium-sized eogyrinid *Pteroplax cornutus* Hancock and Atthey. The only Newsham tetrapod which appears to represent an erratic from a terrestrial/marginal environment is the anthracosaurid embolomere *Anthracosaurus russelli* Huxley.

The structure of the, fish-dominated, open-water/lacustrine community which includes the three endemic Newsham tetrapod species is briefly discussed. Finally, the Newsham assemblage is compared with the only other large, compact tetrapod assemblage of Westphalian B age known, that from Joggins in Nova Scotia. In direct contrast to those known from Newsham, the Joggins tetrapods appear to represent only the more terrestrial elements of the Westphalian B lowland tetrapod fauna of the southern margin of Laurasia. It is therefore suggested that, in view of their close contemporaneity, the assemblages from Newsham and Joggins may be regarded as complementary.

TETRAPOD fossils of Carboniferous age are of rare occurrence and have so far been recorded only from Europe and North America. Within the Westphalian stage of the Upper Carboniferous, only five large, compact tetrapod assemblages are known (A. R. Milner 1980*b*). Two, those from Linton, Ohio, and Nýřany in Czechoslovakia, are of upper Westphalian D age. The assemblage from Jarrow, Eire, is from the middle Westphalian A and the remaining two, from Joggins, Nova Scotia, and Newsham, Northumberland, are both lower Westphalian B in age (data from Rayner 1971, which see for further stratigraphic and palaeoenvironmental details). The Newsham amphibians are of particular importance as constituting the largest taxonomically diverse assemblage of well-preserved tetrapods yet yielded by the Westphalian Coal Measures of the north-west European paralic belt.

Tetrapod specimens from Newsham were first recorded by Kirkby and Atthey (1864), who figured (as '*Rhizodus lanciformis*') a skull fragment of the loxommatid amphibian *Megalocephalus*. Further tetrapod material was described by Hancock and Atthey (1868, 1869*a, b*, 1870*a, b*, 1871*a*), Barkas (1873), Embleton and Atthey (1874), Atthey (1876, 1877, 1884) and Embleton (1889). Much of the loxommatid and eogyrinid material was described by Watson (1912, 1926), who also gave a detailed account of the Newsham keraterpetontid nectridean *Batrachiderpeton* (Watson 1913). With the exception of a short description of the sole recorded Newsham aïstopod specimen by Steen (1938),

subsequent work on the tetrapods from the site has been confined to the past two decades. The eogyrinid embolomeres have been restudied by Panchen (1964, 1966, 1970, 1972) and Boyd (1978, 1980a), *Megalocephalus* by Beaumont (1971, 1977), the keraterpetontid material by A. C. Milner (1978, 1980) and the aïstopod by Boyd (1982a). Specimens representing three taxa hitherto unrecorded from the site have also recently been described. These comprise a lysorophid 'lepospondyl' (Boyd 1980b), the anthracosaurid embolomere *Anthracosaurus* (Panchen 1981), and a urocordylid nectridean (Boyd 1982b).

Most previous publications on the Newsham tetrapods have been morphological and taxonomic studies of individual taxa. Comparison with other Westphalian tetrapod assemblages has been hampered by the fact that the Newsham assemblage has never been reviewed in detail as a single entity and no precise information as to the relative frequency of the species represented has been published. In the present paper the nature of the palaeoenvironment in which the Newsham tetrapods were preserved is considered and the, hitherto unpublished, plant and invertebrate material from the site is briefly described. A revised list of the tetrapod taxa so far recorded from Newsham is given and specimens probably representing three further amphibian taxa are described. A census of Newsham tetrapod specimens follows and an attempt is made to identify ecological associations within the assemblage, employing the methods used by A. R. Milner (1980b) in his study of the Nýřany tetrapods. Finally, the Newsham assemblage is compared with the only other large, compact assemblage of Westphalian B tetrapods known, that from Joggins in Nova Scotia.

The following abbreviations are used for institutions and organizations in this work: BRM, Bradford Museums; BM[NH], British Museum (Natural History); IGS, Institute of Geological Sciences; NCB, National Coal Board; RSM, Royal Scottish Museum, Edinburgh. All specimens referred to by museum registration numbers without one of the above institutional prefixes are in the Hancock Museum, Newcastle upon Tyne.

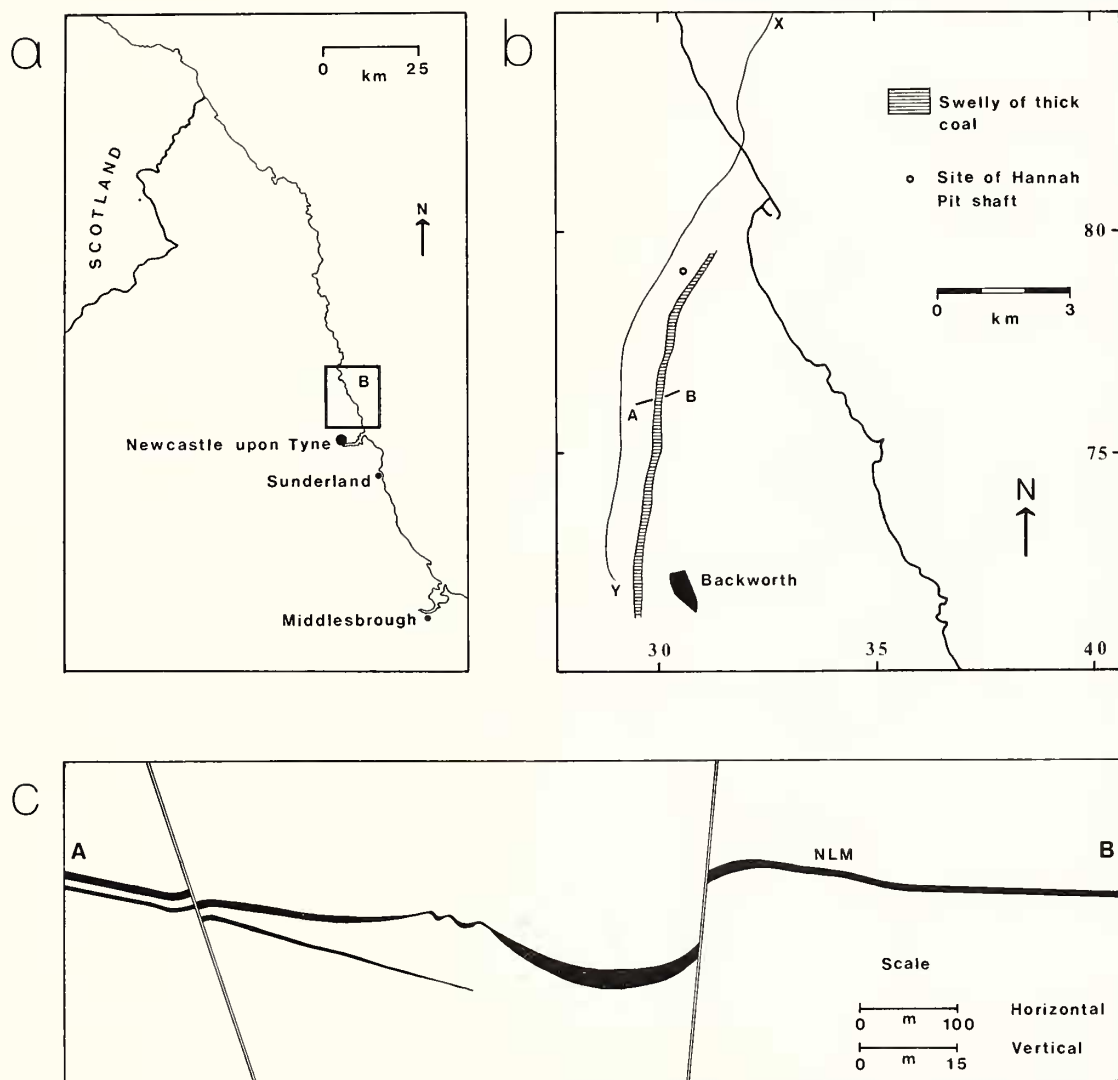
#### PALAEOENVIRONMENT

The Newsham tetrapod assemblage was collected entirely from the workings of Hannah Pit, Newsham Colliery (NZ 306791), which was situated at South Newsham, approximately 1 km south of Blyth in Northumberland. Hannah Pit was sunk in 1860 and remained operational until 1914; however, most of the vertebrate specimens known from the site were collected prior to 1880, by the amateur palaeontologist Thomas Atthey. All are from a bed of black shale immediately overlying the Northumberland Low Main Seam. This horizon lies within the upper *Modiolaris* non-marine lamellibranch zone of the Middle Coal Measures (Land 1974) and is lower Westphalian B in age. During the Westphalian the Newsham area formed a small part of the Pennine depositional province, itself a part of the north-west European paralic belt (Calver 1969).

The shale in which the Newsham tetrapods are preserved is a highly carbonaceous sediment, always well bedded and having, according to Atthey (1877), a thickness of between 7.5 cm and 10 cm. Pyrite is abundant in the shale and is often closely associated with the vertebrate specimens. The presence of pyrite and the high organic content of the shale suggest deposition as an anaerobic sapropel, either in the centre of a lake or during a period of low input of inorganic detritus. As Panchen (1970, p. 66) has noted, the presence of xenacanth and other sharks at Newsham suggests that the surface waters, at least, were adequately oxygenated and the lake may have been thermally stratified, with a warm aerobic epilimnium and a cooler anaerobic hypolimnium.

The lateral extent of the highly fossiliferous area of the black shale worked at Newsham is not certainly known. However, a clue to the nature and extent of the lake in which it was deposited may be afforded by the presence, in the Newsham area, of a linear trough-like 'swelly' of thick coal within the Low Main Seam. The recorded length of this structure, which ranges between approximately 120 m and 185 m in width, extends some 8 km southward from Newsham to the vicinity of Backworth (text-fig. 1b). The 'swelly' appears to terminate at its northern end in the Newsham area, but its southern end has not been explored. The structure of the 'swelly' will be apparent from text-figure 1c. About 0.8 km west of the structure the seam, here between 1.2 m and 1.8 m thick, splits. The lower leaf

thins out completely before reaching the 'swelly'. The upper leaf also thins, to between 0.4 m and 0.9 m, before thickening into the 'swelly' itself (data from Land 1974, p. 59). The 'swelly' has been described by Hurst (1860), who pointed out that strata above and below it are not affected and attributed it to pencontemporaneous deformation, and by Land (1974). The latter, although arriving at no firm conclusion as to the origin of the structure, noted that its direction is in line with that of contemporary depositional currents. Interestingly, Elliot (1965) has described almost precisely similar 'swilleys' [*sic*] within seams in the *Modiolaris* and *Similis-pulchra* zones of the



TEXT-FIG. 1. Location and structure of 'swelly' in Northumberland Low Main Seam. A, Map of north-east England showing area (B) covered by text-fig. 1b. B, Map of the Newsham area showing recorded course of 'swelly' and site of Hannah Pit shaft. Line X-Y indicates course of split in seam to west of 'swelly' (after Land 1974). C, Section through 'swelly' between points A and B on text-fig. 1b. Double lines represent faults (after Hurst 1860). NLM, Northumberland Low Main Seam.



Nottinghamshire Coal Measures. These are convincingly demonstrated by Elliot to represent river courses which became established and were abandoned within the period of deposition of the seams concerned. It seems very likely that the Newsham 'swelly' originated in this manner and that, after reflooding (presumably due to local subsidence) of the old channel to submerge the peat which had accumulated therein since its abandonment, the linear lake thus formed was the environment of preservation of the Newsham tetrapods. It is particularly interesting to note that in the Nottinghamshire Abdy Seam 'swilley' described by Elliot (1965) the thick coal of the 'swilley' trough is roofed by a dark pyritic shale containing fish and lamellibranch fragments. That the trough coal of the Newsham 'swelly' was, at least in certain areas, also roofed by a black shale is evidenced by the strata recorded in the shafts of A and B Pits, Seaton Delaval Colliery (NZ 299 763), which were sunk to the Low Main Seam where it forms the western slope of the 'swelly' trough (Borings and Sinkings 1878-1910, no. 1691).

Unfortunately, it is not certain that the Newsham vertebrates were collected from the roofing shale associated with the thick coal of the 'swelly' trough. The 1893 Abandonment Plan (NCB No. 8566) of the Newsham Colliery Low Main Seam workings indicates that Hannah Pit did work the 'swelly' coal, but the writer has been unable to trace any documentary or other evidence linking the 'swelly' and the vertebrate material. Mining in the area has now ceased, precluding the possibility of examining the 'swelly' underground. However, the occurrence within the workings of one small colliery of a large assemblage of (mostly aquatic) vertebrates and a structure interpretable as an abandoned stretch of river channel is a very remarkable coincidence if the two were not directly associated.

As Panchen (1970) and A. R. Milner (1980*b*) have pointed out, the presence at Newsham of the large embolomere *Eogyrinus* and of crossopterygians up to 6 m long implies a lake large and open enough to sustain the biomass required for the support of such large ultimate consumers. The size of some of the, apparently endemic, vertebrates and the presumed thermal stratification also suggest a water-body of some depth. It will therefore be assumed in the present study that the Newsham vertebrates were preserved in the bottom sediments of a single large lake. However, as Hannah Pit worked approximately the northernmost 1.5 km of the 'swelly's' recorded length it is conceivable that two or more adjacent lakes may have been involved.

*Invertebrates.* The only invertebrate specimens from the Newsham black shale which are known to the writer pertain to ostracods and the bivalve genus *Naiadites*. All are preserved on two small shale slabs, in the Hancock Museum. G162.46 bears several fragmentary *Naiadites* specimens and ostracods representing two species of *Carbonita*; all are too poorly preserved for specific identification. G162.47 bears a single specimen of *Carbonita* cf. *humilis* (Jones and Kirkby) and a second ostracod referable to *Geisina*. The presence of *Carbonita* is of some importance as an indicator of the salinity of the Newsham lake. Whereas *Geisina* is known to have been tolerant of very brackish (and occasionally marine) conditions within the Coal Measures (Calver 1968), *Carbonita* species appear to have been oligohaline, tolerating only fresh to slightly brackish water (Pollard 1966). *Naiadites* species seem to have been euryhaline and Calver (1968) has suggested that the members of this genus may have lived by byssal attachment to floating vegetation. Their presence in the area of deposition of the Newsham black shale, even as living individuals, is thus not necessarily ruled out by the presumed low oxygen tension of the bottom sediments and hypolimnium. None of the, several hundred, specimens of the Newsham black shale examined by the writer shows any convincing evidence of the activity of benthonic invertebrates. In view of the nature of the sediment it is likely that this absence reflects a genuine scarcity of benthonic animal life in the area of its deposition.

*Plants.* The Atthey collection in the Hancock Museum includes a suite of undescribed plant specimens from the Newsham black shale. Of the seventy specimens examined by the writer, fifty-one are determinate at least to generic level. The high proportion of well-preserved, and hence determinate, specimens in the sample may, however, merely reflect collector bias. The taxa present are listed below; the values in brackets indicate the number of specimens present.



LYCOPSIDA	SPHENOPSIDA
<i>Sigillaria tessellata</i> (1)	<i>Calamites cisti</i> (1)
<i>Sigillaria</i> sp. (3)	<i>Calamites</i> sp. (11)
<i>Lepidophloios acerosus</i> (3)	
<i>Lepidodendron aculeatum</i> (3)	PTERIDOSPERMS
<i>Lepidodendron</i> sp. (3)	<i>Trigonocarpus</i> sp. (3)
<i>Lepidostrobus</i> sp. (23)	

With the exception of three *Calamites* specimens (notably G162.45) preserved as pith-casts in a micaceous siltstone, all are compression fossils. The lycopod material, apart from the well-preserved and usually entire strobili, consists of leafy shoots and fragments of large branches. The *Calamites* specimens all represent lengths, mostly less than 10 cm, of stem or branch.

Scott (1977, 1979, 1980) has emphasized the need to relate fossil plant assemblages to depositional environments, and to consider the possible transport history of specimens, before attempting interpretation of the assemblages in terms of the communities they derive from. In the case of the known Newsham plant material it seems likely that most of the specimens represent the flora of the lake margins and have undergone minimal transport. This is suggested by:

1. The well-preserved nature and large size of many of the plant fragments.
2. The relatively large number of intact lycopod strobili.
3. The paucity of taxa represented.

There is, moreover, much evidence to suggest that arborescent lycopods comprised the dominant flora of Westphalian swamp-forests and that *Calamites* grew around the margins of lakes (Scott 1979, 1980).

Nonetheless, the *Calamites* specimens preserved as siltstone pith-casts embedded in the black shale were presumably transported some distance. The same may apply to the pteridosperm seeds; only three are present in the sample and these were probably the parts of the plants in question best suited to surviving transport in a recognizable form. In addition, Scott (1980) has noted that pteridosperms appear to have been characteristic inhabitants of river flood-plains and levée banks in the Westphalian. A swamp-forest or lake margin origin for the Newsham *Trigonocarpus* specimens thus appears unlikely.

The nature of the small lenticular structures from Newsham, described by Hancock and Atthey (1869c) as fungi (*Archagaricon* spp.), is uncertain and the material needs re-study.

*Fishes.* Most of the known Newsham vertebrate material pertains to fishes, which dominate the total assemblage from the site in terms of both number of specimens and number of species represented. Much of the Newsham fish assemblage needs re-study, but a list of twenty-five of the twenty-eight species so far reported from the site has been given by Dr. S. M. Andrews (*in Land* 1974, p. 61); the remaining three species, all haplolepid actinopterygians, were described by Westoll (1944). In addition to the haplolepids, the fish assemblage includes palaeoniscoid and platysomoid palaeoniscids, dipnoans (currently being studied by Dr. T. R. Smithson (University of Newcastle upon Tyne)), rhizodontid and osteolepid crossopterygians, the coelacanth *Rhabdoderma*, climatiid and ischnacanthid acanthodians and a number of elasmobranch genera.

In summary, the environment of preservation of the Newsham tetrapods appears to have been a large and deep freshwater lake of linear shape (but unknown length), occupying a stretch of abandoned river channel in which peat had previously accumulated. Many species of fish inhabited the lake, as did ostracods and, possibly, the bivalve *Naiadites*. The lake was probably surrounded by swamp-forest, composed largely of arborescent lycopods and sphenopsids; the latter may have been especially abundant around the shoreline.

## THE TETRAPOD ASSEMBLAGE

Eight tetrapod species, all amphibians, have so far been described from Newsham:

## Order TEMNOSPONDYLI

Loxommatidae: *Megalocephalus pachycephalus* (Barkas, 1873)

*Note.* The above 'traditional' classification of the Loxommatidae as a family of the Order Temnospondyli is for convenience of listing only, and should not be taken to indicate disagreement with the recent suggestions of Panchen (1980) and Smithson (1982) that the Loxommatidae as a whole should be removed from this order.

Order BATRACHOSAURIA (*sensu* Panchen 1980)

Eogyrinidae: *Pteroplax cornutus* Hancock and Atthey, 1868

*Eogyrinus attheyi* Watson, 1926

Anthracosauridae: *Anthracosaurus russelli* Huxley, 1863

## Order NECTRIDEA

Keraterpetontidae: *Batrachiderpeton reticulatum* (Hancock and Atthey, 1869)

Urocordylidae: *Urocordylid gen. et sp. indet.*

## Order AISTOPODA

Ophiderpetontidae: *Ophiderpeton nanum* Hancock and Atthey, 1868

## Order LYSOROPHIA

Lysorophidae: *Lysorophid gen. et sp. indet.*

However, three further amphibian species from Newsham appear to be represented, each by a single specimen, in the collections of the Hancock Museum. Although none is strictly determinate, even to family level, they will now be described for the sake of completeness.

## Order TEMNOSPONDYLI

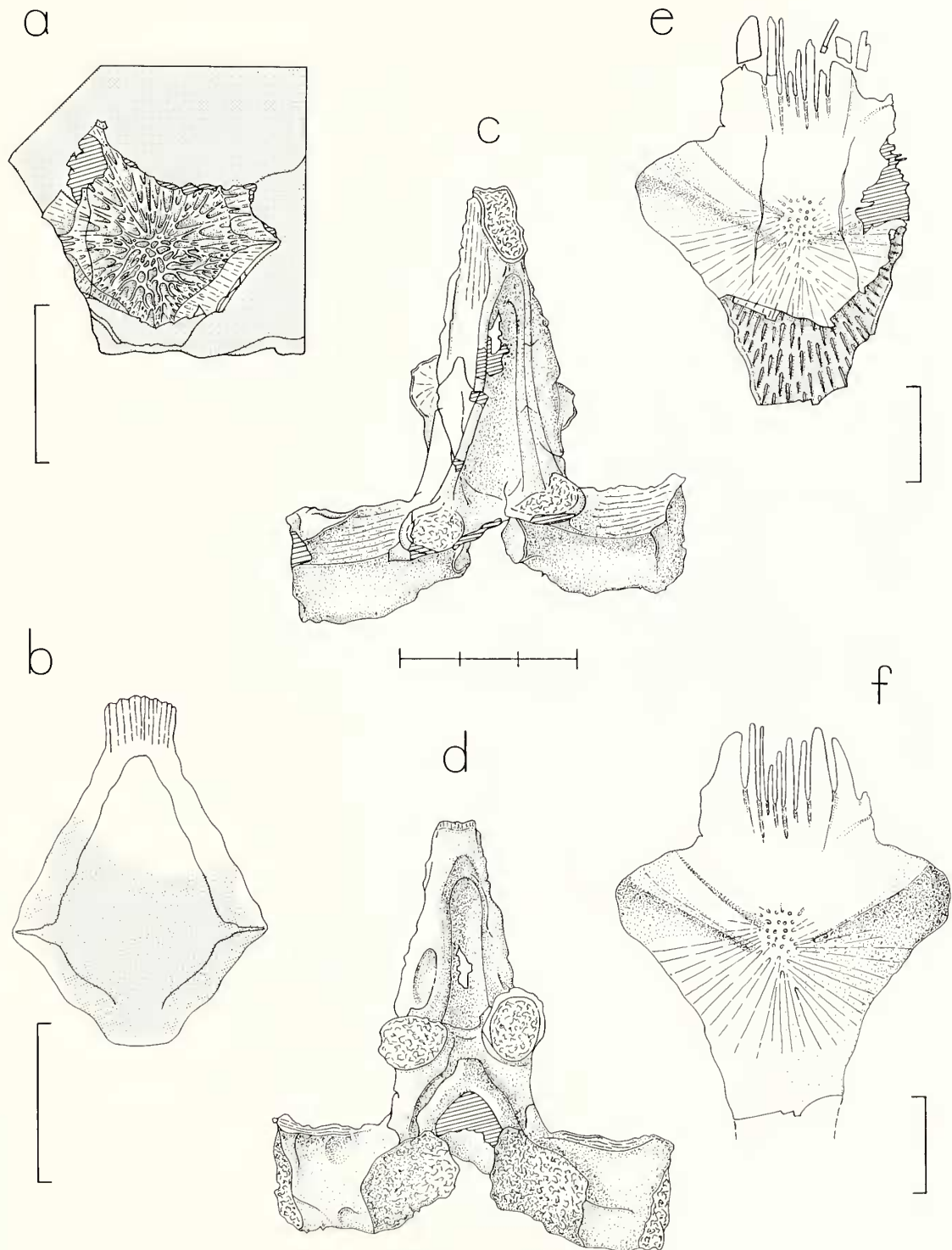
?Colosteidae: colosteid *gen. et sp. indet.*

Specimen G24.98 consists of an incomplete interclavicle preserved with its ventral surface exposed on a small slab of shale (text-fig. 2a). The anterior, posterior and right lateral extremities of the element are absent. The form of the posterior part is, however, apparent from an impression in the matrix and the right lateral extremity may confidently be restored as the mirror-image of the left. Except on the clearly defined, anterolateral, areas of clavicular overlap and on the narrower posterolateral marginal areas, the interclavicle bears a well-developed ornament of pits and ridges radiating from the presumed centre of ossification of the bone. Near the ossification centre, the pits are circular or oval and completely enclosed. Towards the margins of the element, however, the pits become more elongate and are deepest mesially, becoming shallower at their, open, distal ends. Bystrow (1935) has noted that differential growth of ornamented dermal bones produces elongation of the pits in the direction of the greatest growth rate. In G24.98, as preserved, the degree of elongation of the pits is greatest anterior to the centre of ossification, suggesting that the complete bone originally extended further in this direction than posteriorly.

G24.98 does not appear referable to any of the eight previously described Newsham amphibians which are determinate at least to family level. Its size is such that it could only have been derived from a very small juvenile of *Eogyrinus*, *Pteroplax*, *Anthracosaurus* or *Megalocephalus*. However, the nature of the ventral ornament would seem to preclude reference of G24.98 to any of the embolomeres. No certainly associated interclavicle has been described for *Megalocephalus*, but the ornament of G24.98 does not resemble the 'honeycomb' pit and ridge ornament characteristic of much of the dermal skull roof in this genus (Beaumont 1977, fig. 6). In addition, the well-ossified nature of the interclavicle and its well-developed ornament do not suggest that it derives from a very young animal. Nor is it likely that the specimen pertains to any of the four 'lepospondyl' species recorded from

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TEXT-FIG. 2. Isolated skeletal elements of Newsham tetrapods. A-B, Interclavicle G24.98: A, As preserved. Stippling represents matrix; B, Restoration. Stippling represents area actually preserved (ornament omitted). C-D, neural arch G25.03 as preserved: C, Anterior view; D, posterior view. E-F, Interclavicle G94.65. E, As preserved. Stippling indicates area preserved as impression only. F, Restoration. All scale bars graduated in centimetres. Cross-hatching indicates broken bone surface.





Newsham. The interclavicle is not known for adult specimens of *Batrachiderpeton*, but the interclavicle of the juvenile figured by Watson (1913, text-fig. 167 (as '*Ceraterpeton*')) has the form of an antero-posteriorly elongate ovoid. Moreover, the dermal skull roof ornament of adult *Batrachiderpeton* specimens (e.g. Watson 1913, pl. XCVI) is very different from the ornament of G24.98. The Newsham urocordylid, represented in the study sample by only a single vertebra, appears to be a member of the *Ptyonius*-group of Bossy (1976), which comprises the described genera *Ptyonius*, *Urocordylus*, and *Ctenerpeton* (Boyd 1982b). The interclavicles of *Ptyonius* (Bossy 1976, fig. 57b) and *Urocordylus* (Bossy 1976, fig. 77b) are, like those of juvenile *Batrachiderpeton* specimens, ovoid in outline, tapering most acutely to their anterior ends. The ventral ornament in both cases differs from that of G24.98. No interclavicle has been described for *Ctenerpeton* but there is no reason to suppose it to have been radically different in form or ornament from those of *Ptyonius* and *Urocordylus*. Lysorophid limbs and limb-girdles are very small in relation to body size (e.g. Sollas 1920, fig. 1, Carroll and Gaskill 1978, fig. 132B) and G24.98 thus seems far too large to have pertained to a lysorophid of the dimensions of the single Newsham specimen (Boyd 1980b) representative of this group. An interclavicle may have been present in *Ophiderpeton nanum* (Boyd 1982a), but it seems unlikely that G24.98 could have been derived from an individual of this species. Although the only known specimen of *O. nanum* may be a juvenile which could have grown to a size compatible with the possession of an interclavicle of the dimensions of G24.98, the shape of the element tentatively identified as an interclavicle in this form (Boyd 1982a, fig. 1) does not resemble that of G24.98.

Specimen G24.98 does, however, appear closely to resemble the interclavicles known for members of the temnospondyl family Colosteidae. Colosteids have been described from the upper Viséan of Scotland (*Pholidogaster*: e.g. Panchen 1975), the upper Viséan or lower Namurian of West Virginia, U.S.A. (*Greererpeton*: e.g. Carroll 1980; Smithson 1982) and the Westphalian D of Linton, Ohio (*Colosteus*: e.g. Romer 1930). Their occurrence at Newsham would thus not be unexpected from a stratigraphic point of view. Moreover, the Westphalian A tetrapod assemblage from Jarrow, Eire, includes undescribed colosteid specimens, whose dimensions seem roughly compatible with those of G24.98 (A. R. Milner 1980a, p. 135 and pers. comm.).

Among points of particular resemblance between described colosteid interclavicles and G24.98 may be noted:

1. The nature, degree of development and distribution of the ventral ornament (e.g. Carroll 1980, fig. 2).
2. The proportions of the element, partly inferred in the case of G24.98, which extends further anterior to the point of maximum width than posterior to it (e.g. Romer 1930, fig. 8; Carroll 1980, fig. 2).
3. The distinctive shape of the posterior tip of the element, clearly indicated by an impression in the matrix in G24.98 (e.g. Romer 1930, fig. 8). The writer would, therefore, suggest that interclavicle G24.98 probably pertains to a colosteid temnospondyl. The restoration of the element (text-fig. 2b) is based on the form of the interclavicle in *Greererpeton* and *Colosteus*.

#### Order TEMNOSPONDYLI

##### Family *incertae sedis*

Specimen G25.03 is an isolated neural arch (text-fig. 2c-d) which, although otherwise well preserved, has suffered severe antero-posterior compression during preservation. In the course of this compression the anterior face of the arch has been shifted, in the morphologically vertical plane, relative to the posterior face, so that the dorsal edge of the neural spine now slopes downward from posterior to anterior. In addition, the diapophyses have been rotated in such a fashion that their originally antero-dorsal surfaces now face anteriorly.

The height of the neural spine, together with the form and span of the diapophyses, suggest, by comparison with *Eryops* (Moulton 1974), that the arch is that of an anterior dorsal vertebra. The neural spine is a high, narrow structure in its lateral aspect and is deeply excavated both anteriorly and posteriorly by an upwardly tapering groove. Dorsally, the anterior and posterior grooves are linked by a canal piercing the neural spine. The margins of the canal are irregular; whether it is entirely an artefact, produced by breakage of the very thin bone in this region, or a genuine supra-neural canal enlarged by damage to its periphery is uncertain. In view of its small size, the former seems the more likely explanation. The top of the neural spine is slightly expanded and terminates in an originally dorsally-directed, concave facet, whose irregular surface suggests a covering of cartilage in life. The facet may originally have abutted against a dermal ossification. Moulton (1974, p. 15) has noted that the expanded and rugose tips of the dorsal neural spines in mature *Eryops* specimens probably lay in the dermis. He points out, moreover, that in some cases their appearance suggests formation by fusion of the original spine tips with overlying osteoderms. The zygapophyses of G25.03 are large. Unfortunately the *post-mortem* compression of the specimen prevents determination of their original orientation.

Of the eight described Newsham amphibians determinate to family level, only the four 'labyrinthodont' species are large enough to have possessed neural arches of the dimensions of G25.03. The specimen is most unlikely to pertain to any of the embolomeres. The presacral neural spines of *Eogyrinus*, as evidenced by the

vertebrae associated with the lectotype of *E. attheyi* (G13.72), and of *Pteroplax*, as evidenced by the attributed vertebrae described by Boyd (1980a), differ markedly from G25.03. They are relatively short and more massive structures, roughly rectangular in lateral view and lacking expanded tips or dorsal facets. No certainly associated vertebrae have been described for *Anthracosaurus*, but the posterior trunk vertebrae figured by Panchen (1977, fig. 12(a)) as possibly pertaining to *A. russelli* have neural spines resembling those of *Eogyrinus*. Little is known of the vertebrae of *Megalocephalus* or any other loxommatid. However, Baird (1957) described a series of vertebral elements, including apparently five neural arches, associated with a skull of *M. lineolatus* (Cope) from Linton, Ohio. These have been figured by Beaumont (1977, fig. 16b), who has also attributed a very similar, isolated neural arch (G37.88) from Newsham to *M. pachycephalus* (Tilley (Beaumont) 1971, fig. 32). All differ markedly from G25.03 in the possession of narrower neural spines, which appear to lack dorsal facets, and in the size and form of the diapophyses. While it is possible that these differences merely reflect regional variation within the vertebral column of *Megalocephalus*, the evidence at present available is not such as to warrant attribution of G25.03 to this genus.

Of described amphibian neural arches, G25.03 seems most closely to resemble those of the anterior dorsal vertebrae of *Eryops* as figured by Moulton (1974, fig. 2). Points of particular resemblance include the proportions of the diapophyses and the presence, anteriorly and posteriorly, of strongly developed ridges extending dorsally and mesially from the zygapophyses to enclose an upwardly tapering groove in the neural spine. Nonetheless, the neural spines of *Eryops* appear to be somewhat higher than that of G25.03 and, moreover, no diagnostic *Eryops* material of pre-Stephanian age has been described. It is, however, possible that G25.03 pertains to an edopid, rather than eryopid, temnospondyl. *Edops* itself is of lower Permian age and no certainly associated neural spine has been figured. However, edopids occur in the Westphalian D at Linton and Nýřany (A. R. Milner 1980b, p. 463) and the Westphalian A assemblage from Jarrow includes an *Edops*-like form whose vertebrae, since they are apparently rhachitinous in type, may well have borne neural arches not dissimilar to those of *Eryops* (A. R. Milner, pers. comm.). It is interesting to note also that two large rhachitinous vertebrae, in many respects resembling those of *Eryops*, are known from the upper Viséan or lower Namurian of Greer, West Virginia (Smithson 1982, p. 30).

#### Order BATRACHOSAURIA

##### Family *incertae sedis*

Specimen G94.65 is an incomplete interclavicle preserved with its dorsal surface uppermost on a small shale slab (text-fig. 2e). The right lateral and posterior extremities of the element are absent; the shape of at least part of the latter region is, however, apparent from a very clear impression remaining in the matrix. The impression unfortunately terminates abruptly at the edge of the slab, making it impossible to determine with certainty whether or not a parasternal process was originally present. It is apparent from the impression that the ventral surface of the interclavicle bore, at least posteriorly, a weakly developed ornament of elongate shallow pits, presumably radiating from the centre of ossification. The anterior margin of the bone is very markedly fimbriated.

The size of G94.65 is such that, if it were to be referred to any of the eight certainly determinate Newsham amphibians listed above, it could only pertain to a small individual of one of the four 'labyrinthodont' species. No certainly associated interclavicle has been described for *Megalocephalus*, but the ornament of G94.65 could hardly be more different from that of the dermal skull roof of *M. pachycephalus* (e.g. Beaumont 1977, fig. 6). Moreover, the isolated Newsham interclavicle (G13.81) referred to this species by Tilley (Beaumont) (1971, fig. 33) differs from G94.65 in shape, ornament and the absence of a distinctly fimbriated anterior margin. Although the ornament of G94.65 suggests that the specimen pertains to a batrachosaur, rather than a temnospondyl, it is not possible to attribute it with certainty to any of the three known Newsham embolomeres. No certainly attributable interclavicle has been described for *Eogyrinus attheyi* but that present in the holotype specimen of *Pholiderpeton scutigerrum* Huxley, which is probably in fact at least congeneric with the former species, resembles in form the interclavicle of the Permian embolomere *Archeria* as figured by Romer (1957, fig. 1) (J. A. Clack, pers. comm.). It thus differs from G94.65 in both shape and the lack of a 'comb-like' anterior margin. No certainly associated interclavicle has been described for *Pteroplax* or *Anthracosaurus*; the almost total lack of ornament on the dermal skull bones in the latter genus (e.g. Panchen 1977, fig. 1), however, makes it unlikely that G94.65 pertains to this form. While it is just possible that G94.65 derives from a small individual of *Pteroplax*, it must, in the absence of any positive evidence to support such an attribution, be regarded simply as a batrachosaur interclavicle at present indeterminate below ordinal level. The restoration of the specimen (text-fig. 2f) is based upon an assumption of bilateral symmetry and, in part, upon the impression in the matrix.

## CENSUS OF TETRAPOD SPECIMENS

In order to assess the relative abundance of the various tetrapod species represented in the Newsham assemblage a census of specimens from the site has been carried out. Almost all of the known tetrapod material from Newsham is stored in the Hancock Museum (Boyd and Turner 1980), but the census sample also includes specimens in the British Museum (Natural History).

Only specimens referable with some certainty to one of the eight Newsham tetrapod species which are certainly determinate at least to family level have been included in the census sample. The numerous isolated 'labyrinthodont' ribs from the site have thus been excluded. Moreover, the recent recognition of cranial material of *Anthracosaurus* from Newsham (Panchen 1981) means that isolated elements of large embolomeres can no longer be attributed with any certainty to *Eogyrinus*. The large numbers of isolated *Megalocephalus* teeth present in the two museum collections examined for census purposes have also been excluded from the census sample, as many may have been lost in the course of normal tooth replacement during life.

Most of the tetrapod material consists of skulls, isolated skull and postcranial elements or, at best, incomplete articulated skeletons (Boyd and Turner 1980). The assessment of the relative abundance of the taxa present has therefore been made employing the principle of the minimum number i.e. by determining the minimum number of individuals of each species necessary to account for all the specimens referable to that species in the census sample. This method compensates for possible inaccuracies due to one species possessing more skeletal elements, or a more easily disarticulated skeleton, than another (Ager 1963, p. 249).

The results of the census are presented in text-fig. 3; the numbers of individuals of each species estimated to be present in the sample are given in histogram form. A card index comprising details of all 105 tetrapod specimens in the census sample is held by the writer and a copy has been deposited in the Hancock Museum.

## IDENTIFICATION OF ASSOCIATIONS

As A. R. Milner (1980*b*) has pointed out, there are four main types of information inherent in Westphalian tetrapod assemblages, such as that from Nýřany, which permit identification of ecological associations within them:

1. The relative frequency of the various taxa present.
2. The size distribution and degree of articulation of the specimens.
3. The functional morphology of the animals themselves.
4. The environmental and faunal contexts in which the taxa present occur elsewhere.

TAXON	NO. OF SPECIMENS	MINIMUM NUMBER OF INDIVIDUALS IN SAMPLE
<i>Megalocephalus pachycephalus</i>	61	11
<i>Batrachiderpeton reticulatum</i>	21	9
<i>Eogyrinus attheyi</i>	11	4
<i>Anthracosaurus russelli</i>	3	2
<i>Pteroplax cornutus</i>	6	1
<i>Ophiderpeton nanum</i>	1	1
Lysorophid gen. et sp. indet.	1	1
Urocordylid gen. et sp. indet.	1	1

TEXT-FIG. 3. Results of census of Newsham tetrapods.



On the basis of the above types of information, Milner recognized three associations, derived from different environments, within the Nýřany assemblage. These associations, which were further defined by Milner (1980*b*, pp. 471–473) in terms of the most consistently occurring tetrapod families characteristic of each at Nýřany and other Westphalian sites, comprised:

1. A terrestrial/marginal association, characterized by dendrerpetontid and dissorophid temnospondyls (the latter family apparently replacing the former in post-Westphalian B localities), gymnarthrid, hapsidopareiontid and tuditanid microsaur, romeriid captorhinomorphs, and ophiacodontid pelycosaur.
2. A shallow-water/swamp-lake association, characterized by ophiderpetontid aistopods and urocordylid neotridaeans.
3. An open-water/lacustrine association, characterized by loxomatids and eogyrinid embolomeres.

Using the four types of information listed above, the Newsham tetrapods may also be divided into three ecological associations, derived from different environments.

1. *Terrestrial/marginal association.* The terrestrial/marginal 'association' known from Newsham appears to include only *Anthracosaurus russelli*, represented in the census sample by three specimens. The specimens comprise the incomplete left mandibular ramus (G24.35) described by Panchen (1981), an undescribed right jugal (G24.39) noted by Boyd and Turner (1980, p. 13) and an isolated skull table (G13.78). The skull table was originally figured by Atthey (1877, pl. XIII) as that of *Pteroplax cornutus*, but was later referred by Watson (1926) to *Eogyrinus attheyi*; the latter attribution was endorsed by Panchen (1970, 1972). However, comparison of G13.78 with the skull table of the holotype of *A. russelli* indicates that it actually pertains to this species (J. A. Clack, pers. comm.). Its almost unornamented dorsal surface is thus not due, as has been suggested (Panchen 1964), to *post-mortem* erosion but is probably merely characteristic of *Anthracosaurus* (e.g. Panchen 1977, fig. 1). At least two individuals are represented by the three Newsham *Anthracosaurus* specimens. The jaw ramus apparently derives from a somewhat smaller animal than is represented by the, 40 cm long, holotype skull of *A. russelli* (Panchen 1981, p. 89), but the jugal and skull table are closely similar in size to those of the holotype. They could, therefore, both be derived from one individual.

No certainly associated post cranial remains have been described for *A. russelli* but several aspects of its known cranial morphology suggest that the adults, at least, may have been largely terrestrial in habit. Thus, the skull is massively built and reptiliomorph in appearance, with orbits facing more laterally than is the case in *Eogyrinus*, and lateral line sulci are absent save for possible traces on the jugals. Naso-labial grooves, regarded by Panchen (1967) as probably primitive for tetrapods and serving, in conjunction with ventrally placed external nares, to keep the buccal cavity free of excess water, are absent. The teeth are massive, roughly conical structures and are recurved to a much lesser extent than those of the, probably largely piscivorous, *Eogyrinus* (data from Panchen 1977). Moreover, the mid-point of insertion and line of action of the adductor muscles of the lower jaw were further forward in relation to the tooth row in *Anthracosaurus* than in *Eogyrinus*, increasing the static pressure capable of being exerted on prey items when the jaw was near closure (Panchen 1981). Olson (1961) has suggested that the static pressure system of jaw closure was originally developed in tetrapods as an adaptation to terrestrial feeding, upon invertebrates such as insects and molluscs. It seems likely, however, that adults of *Anthracosaurus* fed also upon other tetrapods, possibly around the margins of lakes and rivers.

Specimens of *A. russelli*, the sole known member of the family Anthracosauridae, have been described only from the Westphalian of England and Scotland (Panchen 1977); no certainly anthracosaurid material has been reported amongst the tetrapod assemblages from Linton, Nýřany, Jarrow, or Joggins. The absence of anthracosaurids from the Joggins assemblage, which is almost precisely contemporary with that from Newsham and is composed primarily of terrestrial tetrapods, is of some interest and is discussed elsewhere in the present study (see below).

In summary, the relative rarity of *A. russelli* specimens in the census sample and the functional

morphology of the animal, so far as it is known, suggest that this species was not endemic in life to the environment of preservation of the Newsham tetrapods. It is presumed to have formed part of a terrestrial/marginal tetrapod community, of which it is the only representative so far known from the site (text-fig. 4). While it is possible that the Newsham *A. russelli* material, which all appears to pertain to adult animals, is derived from individuals which were visiting the lake to breed, the fragmentary nature of the known specimens suggests rather that they are erratics, having been transported to the site *post-mortem*.

2. *Shallow-water/swamp-lake association*. The three Newsham tetrapods regarded with some confidence as comprising this association are the ophiderpetontid aïstopod *Ophiderpeton nanum*, a urocordylid nectricean and a lysorophid. Each is represented by only a single specimen in the census sample. The urocordylid and the lysorophid are not certainly determinate below family level.

The specimen of *Ophiderpeton nanum* consists of a poorly preserved skull and incomplete postcranial skeleton, the latter including the most anterior forty-three vertebrae in an articulated series (Boyd 1982a, fig. 1). The vertebral count in an entire specimen of this species is not known, but Baird (1964, p. 6) has given a figure of 100 + for a juvenile of *O. granulosum* Fritsch. The first forty vertebrae of the *O. nanum* specimen together measure 11.2 cm; on the assumption the vertebral count of the complete animal was similar to that of *O. granulosum*, the total length of its vertebral column may very roughly be estimated at somewhat in excess of 28 cm. The skull appears to have been approximately 1 cm in length.

A restoration of the probable appearance of *Ophiderpeton* in life has been published by A. R. Milner (1980b, fig. 5). The body in this genus is highly elongate and snake-like, and the tail very short (Zidek and Baird 1978). Although an interclavicle may be present in the Newsham *O. nanum* specimen (Boyd 1982a), there is no convincing evidence of the presence of limbs in any described aïstopod (Baird 1964; Wellstead 1982). The skull of *Ophiderpeton* is narrow and elongate with the orbits placed well forward, anterior to large temporal fenestrae (Steen 1931; Thomson and Bossy 1970). The body bears a ventral armour of elongate, needle-like gastralia arranged *en chevron*, and the dorsal and lateral surfaces of both body and tail are covered by an armour of small, pebble-like osteoderms. The latter armour also extends forward to cover the temporal fenestrae (Baird 1964). Examination of a skull (BM(NH) R2657) of *O. amphiuminum* (Cope) from Linton indicates that the small marginal teeth are not, as described by Steen (1931), merely erect and cylindrical, but possess horizontal chisel-like edges and resemble in form those of the lower Permian embolomere *Archeria* (e.g. Panchen 1970, fig. 4b). Like those of *Archeria*, the marginal teeth of *Ophiderpeton* appear to have been closely set and of roughly uniform height over most of the length of the tooth row. As A. R. Milner (1978) has pointed out, such a dentition provides a continuous surface for gripping, rather than piercing, prey and it is probable that *Ophiderpeton* fed largely upon soft-bodied invertebrates considerably smaller than itself. While it is clear that *Ophiderpeton* had a lateral undulatory propulsive system (Lund 1978), conflicting opinions have been expressed as to the primary environment in which the system was used. Thus, Romer (1930) considered that both phlegethontiïd and ophiderpetontid aïstopods were entirely aquatic whereas Gregory (1948) argued for a burrowing mode of life for *Ophiderpeton*, and Thomson and Bossy (1970) merely noted that, whether on land or in water, aïstopods obviously 'swam'. However, as A. R. Milner (1980b) has noted, *Ophiderpeton* has not been reported from any primarily terrestrial tetrapod assemblage but is of frequent occurrence at Jarrow, Linton, and Nýřany. Furthermore, at the latter two localities this genus would appear, from published data (Romer 1930, p. 140; A. R. Milner 1980, p. 454), to be considerably more abundant than the phlegethontiïd aïstopod *Phlegethontia*, which has been convincingly demonstrated by Lund (1978) to have been primarily terrestrial. Thus, although the serpentiform body, short tail, small orbits and heavy dermal armour of *Ophiderpeton* may indicate derivation from burrowing ancestors it would seem likely that the known members of this genus were very largely, if not entirely, aquatic in habit. Gregory's (1948) objection to an aquatic mode of life for *Ophiderpeton*, on the grounds that the caudal vertebrae lack the high neural and haemal spines seen in the tail of urocordylid nectriceans,

seems of little moment. In *Ophiderpeton* the trunk is very elongate and the tail short (Zidek and Baird 1978) whereas the reverse of this arrangement is exhibited by the urocordylids, in which the tail is markedly longer than the trunk (A. C. Milner 1980) and clearly constituted the major propulsive organ in aquatic locomotion. It is, moreover, possible that the posterior body and tail of *Ophiderpeton* species bore dorsal and ventral fin-like membranes without skeletal supports, such as are present in some (almost tailless) aquatic apodans of the family Typhlonectidae. Indeed, *Ophiderpeton* species may parallel the typhlonectids in being secondarily aquatic, limbless amphibians derived from ancestors adapted for a burrowing mode of life.

The presumed mode of life of *Ophiderpeton*, the presence of only a single specimen at Newsham and the relative abundance of this genus at Jarrow, Linton, and Nýřany together suggest that *O. nanum* was not endemic in life to the environment of preservation of the Newsham tetrapods but is to be regarded as probably an erratic derived from a shallow-water/swamp-pool environment. The poorly preserved and incomplete nature of the specimen may indicate *post-mortem* transport (text-fig. 4).

The Newsham urocordylid specimen is an isolated posterior caudal vertebra which, although indeterminate at generic level, appears, as noted above, to pertain to a member of the *Ptyonius*-group of Bossy (1976). Comparison with the caudal vertebrae of the *Urocordylus wandesfordii* holotype as figured by Bossy (1976, fig. 73), which measures approximately 55 cm in total length, suggests that the Newsham vertebra derives from an animal of closely similar size. Like other urocordylids, the *Ptyonius*-group members were principally, if not entirely, aquatic in habit, swimming by sinusoidal flexure of the body and long laterally compressed tail (A. C. Milner 1980). *Ctenerpeton* is known only from the posterior trunk and tail, but in *Urocordylus* and *Ptyonius* the trunk was shorter than in the *Sauropleura*-group urocordylids (*Sauropleura*, *Lepterpeton*, and *Crossotelos*: Bossy 1976), having a maximum of twenty-two vertebrae. The tail, which in *Urocordylus* includes over eighty vertebrae, was particularly deep in vertical profile, being of constant depth for the anterior two-thirds of its length and then tapering rapidly to its tip (A. C. Milner 1980, after Bossy 1976). Bossy (1976) has suggested that *Urocordylus* and *Ptyonius* were adapted for sustained powerful swimming, although having a lower initial acceleration than the *Sauropleura*-group genera. The skull of *Ptyonius*-group urocordylids is adequately known only in *Ptyonius* itself, but that of *Urocordylus*, as restored by Bossy (1976), appears similar in being broader and shorter-snouted than is the case in the *Sauropleura*-group. Cranial kinesis in *Ptyonius* was apparently restricted to the supratemporal-squamosal line and Bossy (1976) suggests that the jaw mechanics of this genus tended towards the static-pressure system of Olson (1961), thus differing from the specialized type of kinetic inertial system found in *Sauropleura* and its allies. The teeth of *Ptyonius* are smaller and more numerous than those of *Sauropleura* and differ also in not being recurved. It thus seems likely that *Ptyonius*-group urocordylids were adapted for feeding on relatively smaller and less vigorous prey than that of *Sauropleura*-group members, and their diet may have consisted in large part of soft-bodied invertebrates.

Although rare at Newsham, urocordylids are relatively abundant at Nýřany (at least thirty-two specimens of *Sauropleura scalaris* Fritsch), Linton (many specimens of *Sauropleura pectinata* Cope, at least eight specimens of *Ctenerpeton remex* Cope and at least fifteen specimens of *Ptyonius marshii* (Cope)) and at Jarrow (four specimens of *Urocordylus wandesfordii* Wright and Huxley and two specimens of *Lepterpeton dobbsii* Wright and Huxley) (data from A. C. Milner 1980). It is therefore probable that, although known urocordylids were clearly largely aquatic in habit, the species represented by the single Newsham specimen was not endemic in life to the environment in which the Newsham tetrapods were preserved but is an erratic from a shallow-water/swamp-pool environment (text-fig. 4). The nature of the specimen suggests that transport to the site of preservation may have been *post-mortem*.

The lysorophid specimen from Newsham consists of twenty-one articulated vertebrae, apparently from the anterior trunk region, most of which are associated with their respective rib pairs (Boyd 1980b, fig. 1A). The vertebrae are almost identical in size with the anterior trunk vertebrae of the *Lysorophus* specimen described by Sollas (1920), which has a skull length of slightly less than 2 cm.



Seventy-two presacral vertebrae are present in the articulated specimen of *Cocytinus* figured by Carroll and Gaskill (1978, fig. 132B). On the assumption that a similar number was originally present in the animal represented by the Newsham specimen, the length of its presacral vertebral column may very tentatively be estimated at approximately 35 cm, although this makes no allowance for regional variation in centrum length. The snout-vent length of the Newsham lysorophid was thus probably about 37 cm and, if the tail was like that of *Lysorophus* (Olson 1971) in being roughly one-sixth as long as the body, the overall length would have been in the region of 43 cm.

The known lysorophids were apparently largely aquatic, although Olson (1971) has suggested that *Lysorophus* may have been capable of some overland travel by wriggling. Lysorophid limb girdles and limbs are very small relative to body size (e.g. Sollas 1920, fig. 1; Carroll and Gaskill 1978, fig. 132B) and the latter were probably functionally insignificant in both aquatic and terrestrial locomotion. There is little doubt that the animals were active swimmers, moving by sinusoidal flexure of the long body and short, laterally compressed, tail. The skull is completely open in the orbital and temporal regions (Sollas 1920) suggesting that lysorophids were not habitual burrowers; the presence of *Lysorophus* specimens preserved in aestivation burrows in the lower Permian of Oklahoma (Olson 1971) does, however, indicate some capability in this respect. As Olson (1971) has pointed out, the ability to aestivate would also seem to suggest that, although lysorophids exhibit well-ossified branchial arches and may have been perennibranchiate, functional lungs were also present. Lysorophid premaxillae and maxillae were freely moveable on the rest of the skull (Carroll and Gaskill 1978) and the teeth of *Lysorophus* are relatively large, few in number and slightly recurved (Sollas 1920, fig. 38). It would thus seem likely that lysorophids were active carnivores, feeding on relatively large and vigorous prey. Coprolites containing the bones of a small temnospondyl, a small captorhinomorph reptile and palaeoniscid fishes, in addition to lamellibranch shells, have been attributed to *Lysorophus* by Olson (1971). As Olson notes, insects and various aquatic invertebrates doubtless also formed part of the diet of *Lysorophus*, which probably had a mode of life in many respects similar to that of the extant urodele *Amphiuma*.

The presence of only a single, incomplete, lysorophid in the census sample and the inferred mode of life of the members of the group together suggest that the Newsham specimen was derived from an aquatic environment other than that in which it was preserved. Lysorophids have been reported from few localities in the Westphalian. They do, however, occur at Linton, where the group is represented by the genera *Molgophis* and *Cocytinus* (Steen 1931), and may also be present at Jarrow (Carroll and Gaskill 1978, p. 187), although the poor preservation of the material from the latter site makes identification uncertain. It thus seems likely that the Newsham lysorophid specimen represents an erratic transported from a shallow-water/swamp-lake environment (text-fig. 4). A. R. Milner (1982, p. 661) has suggested a similar origin for the single *Cocytinus* specimen recorded as part of the Westphalian D tetrapod assemblage from Mazon Creek, Illinois.

Two further Newsham amphibian taxa may also, although less certainly, represent erratics from shallow-water/swamp-lake environments. The first is the medium-sized, almost certainly eogyrid, embolomere *Pteroplax cornutus*, apparently represented in the census sample by six specimens. Of these, only the isolated skull table (G15.72) designated the lectotype of *P. cornutus* by Romer (1963) is certainly referable to this species. However, as the five attributed specimens could all, in theory, be derived from the same individual as the lectotype, the slight uncertainty as to their pertaining to *P. cornutus* does not affect the assessment of the minimum number of individuals represented by the material. The attributed specimens comprise: a trunk pleurocentrum, intercentrum and one indeterminate central element in association with two neural arches and three ribs (G83.68); seven articulated trunk vertebrae in association with four ribs (G15.73); a caudal intercentrum (G4.83); an isolated left pterygoid (G25.45) and a right nasal with associated premaxilla (G24.40). The last specimen is, if correctly attributed to *P. cornutus*, of some importance as the premaxilla bears four recurved teeth (Boyd 1978, fig. 10) of the shape characteristic of eogyrid, rather than archeriid or anthracosaurid, embolomeres (Panchen 1970). Reasons for attributing the above five specimens to *P. cornutus* have been set forth elsewhere (Boyd 1978; 1980a). There can be little doubt that *P. cornutus* was largely aquatic: the skull table bears well-developed lateral line sulci (Panchen 1970, fig. 14A), as

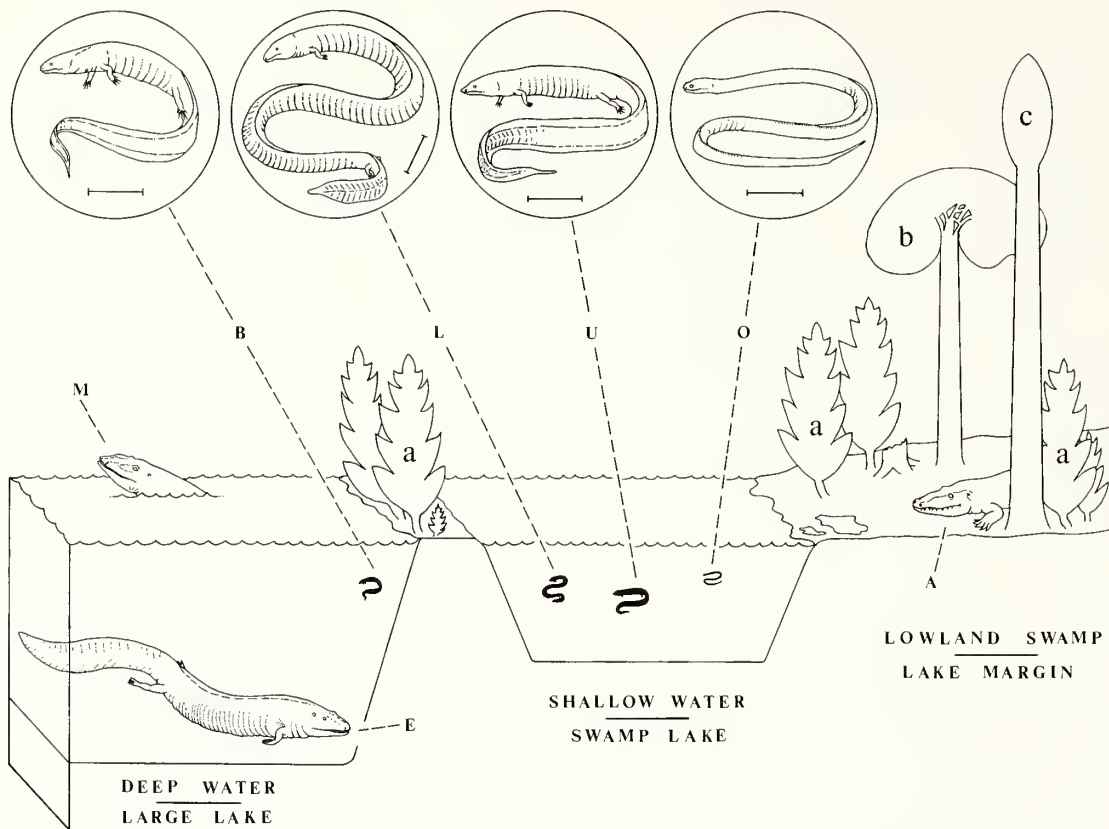
do the attributed nasal and premaxilla. The structure and mode of life of eogyrinid embolomeres have been discussed by Panchen (1970; 1972), who regards the members of this family as aquatic carnivores, swimming in anguilliform manner by sinusoidal flexure of the elongate body and long, laterally compressed, tail. The teeth of *P. cornutus*, if correctly attributed to this species, suggest a piscivorous habit. The inferred mode of life of *P. cornutus*, its rarity at Newsham and the nature of the few specimens known from the site together suggest the possibility that the species may not have been endemic to the environment of preservation but represents an erratic from another aquatic environment, possibly of the shallow-water/swamp-lake type. A second and, in view of the rarity of embolomere specimens at Nýřany (A. R. Milner 1980*b*) and Linton (Panchen 1977), perhaps more likely possibility is that *P. cornutus* was primarily a river-dwelling species.

If the isolated amphibian interclavicle (G24.98) described above as probably that of a colosteid temnospondyl is correctly so designated, it too may represent a transported erratic from a shallow-water/swamp-lake environment. Described colosteids were clearly largely aquatic in habit: the skull bore a well-developed lateral line system (e.g. Romer 1930, fig. 11; Smithson 1982, fig. 7) and the vertebral column, where known, includes approximately forty presacral vertebrae (Smithson 1982, p. 31). Colosteids have not been reported from any primarily terrestrial tetrapod assemblage, such as that from Jogjins, and in the Westphalian occur at Jarrow and Linton (A. R. Milner 1980*a*, p. 135; Romer 1930).

As A. R. Milner (1980*b*) has pointed out, the haplolepid actinopterygians known from Newsham are probably also to be regarded as erratics from a shallow-water/swamp-lake environment. Haplolepid is rare at Newsham: Westoll (1944) described the remains of only four individuals, representing three species, from the site. The haplolepid-aïstopod-nectridean 'facies fauna' of Westoll (1944) has been equated by A. R. Milner (1980*b*, p. 474) with the latter's shallow-water/swamp-lake association and redefined, in more precise terms, as a haplolepid-ophiderpetontid-urocordylid association. However, the recent recognition of urocordylid material from Newsham (Boyd 1982*b*) means that, despite Milner's more restricted definition of the haplolepid 'facies fauna', Westoll's (1944) statement that members of all three constituent groups occur as occasional individuals at the site still holds true.

3. *Open-water/lacustrine association.* The three Newsham tetrapod species regarded as comprising this association, and as having been endemic in life to the environment of their preservation, are *Megalocephalus pachycephalus*, *Batrachiderpeton reticulatum*, and *Eogyrinus attheyi*. These are the most abundant species in the census sample, each being represented by more than ten specimens (text-fig. 3).

*Megalocephalus pachycephalus* is the most frequent tetrapod in the sample studied. Sixty-one specimens are present, representing the remains of at least eleven individuals. Interestingly, all the Newsham material certainly referable to *M. pachycephalus* consists of skulls, skull fragments, isolated cranial elements, and teeth (Boyd and Turner 1980), although a few postcranial bones from the site have been attributed to this species. The latter comprise an isolated neural arch (G37.88), an interclavicle (G13.81) and an ilium (RSM 88.33) figured by Tilley (Beaumont) (1971, figs. 32–34), and a number of isolated centra figured in part by Panchen (1980, fig. 9*d–e*). In view of the relative abundance of *M. pachycephalus* at Newsham, the absence of certainly associated postcranial remains is somewhat surprising. However, a similar state of affairs has been noted by A. R. Milner (1980*b*, p. 448) at Nýřany, where many of the medium to large amphibian specimens consist only of isolated skulls or skulls in association with disarticulated pectoral elements. Milner suggests that this is due to the combination in the animals concerned of a large dense skull and pectoral girdle anteriorly and a potentially autolysing hind-gut posteriorly, resulting in the bodies and tails of the corpses disintegrating or floating away while the denser anterior ends remained stationary. The almost total lack of even isolated postcranial material plausibly referable to *M. pachycephalus* at Newsham may conceivably be due to most of the floating, headless, bodies having been carried from the lake by excurrent streams. Alternatively, many of the 'missing' postcranial elements may be preserved in areas of the Newsham black shale which have not been collected.



TEXT-FIG. 4. Restorations of tetrapod taxa recorded from Newsham. The animals are depicted in diagrammatic representations of the environments they are considered to have inhabited in life. Abbreviations: M—*Megalosaurus* (after A. R. Milner 1980b, fig. 3), B—*Batrachiderpeton* (postcranial proportions based on those of *Keraterpeton* as figured by A. C. Milner 1980, fig. 4A). Scale bar represents 5 cm, E—*Eogyrinus* (after A. R. Milner 1980b, fig. 3), L—lysorophid (proportions based upon those of *Cocytinus* skeleton figured by Carroll and Gaskill 1978, fig. 132B). Scale bar represents 3 cm, U—urocordylid (restoration based upon skeleton of *Urocordylus* as figured by Bossy 1976, fig. 73). Scale bar represents 6 cm, O—*Ophiderpeton* (after A. R. Milner 1980b, fig. 5). Scale bar represents 3 cm, A—*Anthracosaurus* (postcranium hypothetical). Plant symbols partly after Scott (1979). Abbreviations: a—*Calamites*, b—*Lepidodendron*, c—*Sigillaria*.

The total lengths of the Newsham *M. pachycephalus* skulls in which such measurement is possible range between approximately 35 cm and 40 cm, although the dimensions of one incomplete specimen (BM(NH) R3417) are suggestive of an even greater original length (Beaumont 1977). The presence at the site of sub-adult individuals of the species is suggested by an isolated right jugal (G140.81) measuring only 72 mm in length; that of the roughly 35 cm long, skull figured by Beaumont (1977, fig. 8) measures approximately 150 mm. The skull of *M. pachycephalus* is crocodile-like in shape and bears well-developed lateral line sulci, suggesting that the animal spent a considerable amount of time in water. Such a habit is also suggested by the ventrally placed external nares, which are separated from the jaw margin by distinct naso-labial grooves (*sensu* Panchen 1967, p. 413). The slender, lanceolate marginal teeth of *M. pachycephalus*, the shagreen of denticles on the parasphenoid and dermal palatal elements and the kinetic inertial system of jaw closure (Beaumont 1977) all suggest that this species was an aquatic feeder and probably largely piscivorous. Although it is possible that,



as A. R. Milner (1980*b*) has suggested, loxommatids such as *Megalocephalus* lived a crocodile-like existence, entering the water to feed but otherwise resting around lake and river margins, the large amount of *M. pachycephalus* material from Newsham might be taken to indicate a more thoroughly aquatic mode of life for this species at least. Loxommatids appear to occur only rarely in tetrapod assemblages from shallow-water/swamp-lake environments. Thus, A. R. Milner (1980*b*) reported only one specimen representative of this family, a skull of *Baphetes*, amongst approximately 400 tetrapod specimens from Nýřany. Beaumont (1977) listed only five loxommatid specimens from Linton and one, a *Megalocephalus* skull, from Jarrow; the second Jarrow skull (BM(NH) R8465) cited by Beaumont, and considered by her to be possibly that of a juvenile *Megalocephalus* specimen, actually pertains to the aïstopod *Ophiderpeton* (A. R. Milner, pers. comm.).

*Batrachiderpeton reticulatum* is the second most frequent tetrapod species in the census sample; twenty-one specimens are present, representing at least nine individuals. Both adults and juveniles are represented in the material (Boyd and Turner 1980, pp. 18–19) and there appears to be a correlation between the size and degree of disarticulation of the specimens. The adult *B. reticulatum* material consists almost entirely of isolated skulls, skull fragments and isolated mandibular rami and vertebrae, although in one specimen (G25.39) part of the pectoral girdle is associated with an incomplete skull. Of the four juvenile specimens, however, two consist of skulls in association with much of the postcranial skeleton. This size-linked disintegration may have been a result of the larger animals having had a greater, potentially autolysing, volume of hind gut, capable of producing more gas before decomposition was inhibited by the anaerobic conditions on the lake bottom (A. R. Milner 1980*b*, p. 448). Like all other known keraterpetontid neotridae, *B. reticulatum* was clearly largely, if not entirely, aquatic in habit, swimming by sinusoidal flexure of the body and the long, laterally compressed tail. The skull, which in the restoration figured by A. C. Milner (1980, fig. 5*f*) measures approximately 5 cm in length, is short-snouted with an akinetic skull table firmly sutured to the, relatively deep, cheek region. The marginal teeth are of moderate size and conical in form, with incurved tips. Teeth only slightly smaller are present on the coronoids and the lateral dermal palatal elements; in addition, the pterygoids bear a shagreen of denticles anteriorly. The mandible bears a well-developed retroarticular process (data from A. C. Milner 1980). A. C. Milner (1978; 1980) has suggested that the jaw mechanism of keraterpetontids tended towards the static pressure type and that the animals were adapted for seizing and crushing small invertebrates with shells or hard exoskeletons. *B. reticulatum* appears to have possessed a, probably ligamentous, connection between the tabular horn and cleithrum on each side; these connections probably served to dampen lateral oscillatory movements of the head during swimming and thus to facilitate a straight-line approach to prey (A. C. Milner 1980, p. 389). It seems quite probable that, as A. R. Milner (1980*b*, p. 477) has suggested, this species lived around the margins of the Newsham lake, possibly in stands of marginal vegetation including *Calamites*.

The relative abundance of *B. reticulatum* at Newsham and the nature of the known material both strongly suggest that this species was endemic to the site. Indeed, A. R. Milner (1980*b*) has suggested that keraterpetontids should be regarded as forming part of the Westphalian open-water/lacustrine tetrapod association, although not occurring uniformly enough with loxommatids and eoogyrid embolomers to be included with the latter two taxa in the familial characterization of this association. Keraterpetontids are absent from Nýřany (A. R. Milner 1980*b*) and rare at Linton (only eight reported specimens of *Diceratosaurus brevisrostris* (Cope): A. C. Milner 1980, p. 404). At least twenty-four specimens of *Keraterpeton galvani* Wright and Huxley are known from Jarrow (A. C. Milner 1980) but A. R. Milner (1980*b*, p. 473) interprets these as constituting a 'juvenile swarm' and, presumably, as inhabiting a water body shallower than those preferred by the adults.

*Eogyrinus attheyi* is represented in the census sample by eleven specimens; these include the remains of at least four individuals. All the specimens in the sample, with the exception of the lectotype of *E. attheyi*, are skull fragments and isolated cranial elements. The lectotype consists of an almost complete skull with both mandibular rami (Panchen 1972, fig. 2), in association with at least twelve anterior trunk vertebrae, six ribs, a number of dermal scutes and a limb bone interpreted by Panchen (1972) as a femur. The presence of only a few anterior vertebrae with the lectotype skull and

the absence of associated postcranial remains with the other *E. attheyi* skull specimens may, as has been suggested in the case of the Newsham loxommatid material, be due to the disintegration or floating away of the, less dense, postcrania as a result of gas generation by hind-gut autolysis. As has been noted above, the, fairly numerous, isolated elements of large embolomere vertebrae from Newsham (e.g. Boyd & Turner 1980, pp. 13–16) have been omitted from the census sample on the grounds that some may pertain to *Anthracosaurus russelli* rather than *E. attheyi*. The same applies to the large isolated dermal scutes (e.g. Panchen 1972, fig. 15) from the site. However, even if most or all of these vertebrae and scutes are in fact derived from *E. attheyi*, as is statistically likely to be the case, they are not sufficient in number for their exclusion from the study sample to make any difference to the assessment of the minimum number of individuals of this species based upon skull material.

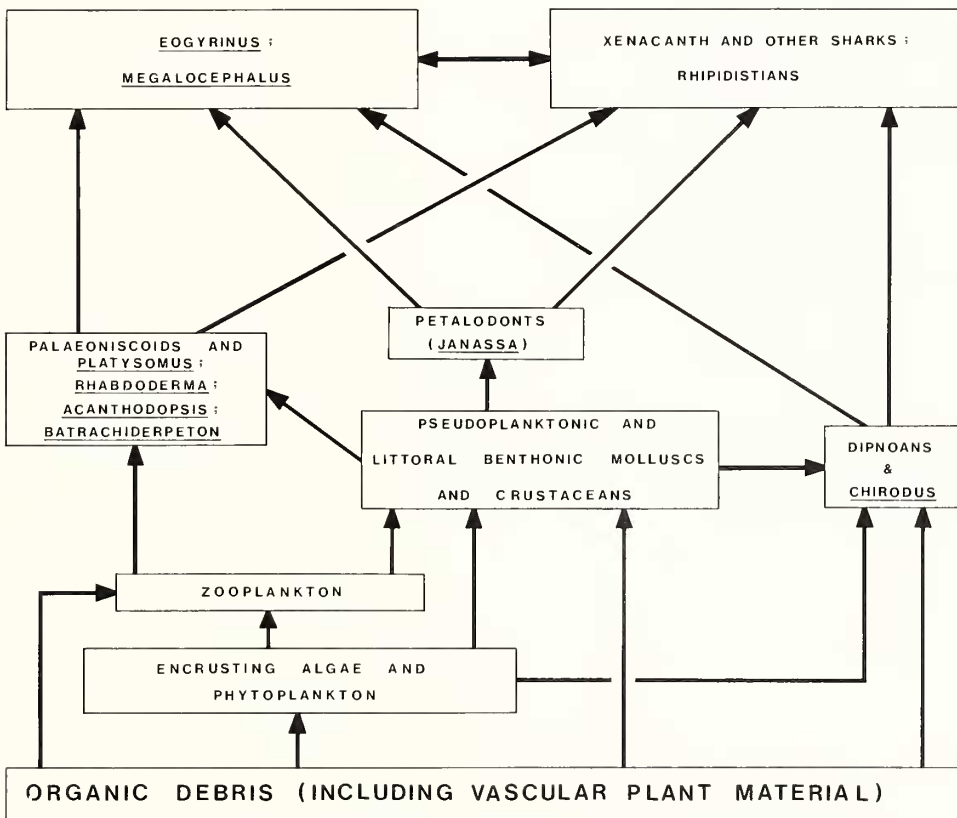
*E. attheyi* was probably the largest of the apparently endemic Newsham tetrapods and one of the largest vertebrates known from the site; the lectotype skull has an overall length of 41 cm and the complete animal may have been up to 4 m long (Panchen 1972). The fact that this species is apparently much less abundant at Newsham than are *Megalocephalus* and *Batrachiderpeton* is consistent with its greater size and presumed status as an ultimate consumer. The skull bears well-developed lateral line sulci and naso-labial grooves are present below the external nares; there can thus be little doubt that *E. attheyi* was, as suggested by Panchen (1970), largely aquatic in habit, swimming by sinusoidal flexure of the elongate body and long, deep, tail. The marginal teeth are of moderate size and recurved at their tips. A row of similar teeth is present on each ectopterygoid, which, like the palatine, bears tusks anteriorly. The form of the teeth and the shagreen of tiny denticles on the pterygoids and coronoids are suggestive of a diet largely of fish and the presence in *E. attheyi* of a kinetic inertial system of jaw closure (Panchen 1970) might be taken to indicate that aquatic feeding was the norm for this species. Moreover, as Atthey (1876, p. 165) pointed out, amongst the vertebrae and ribs associated with the *E. attheyi* lectotype are preserved a toothplate, rib, and several scales referable to the dipnoan genus *Ctenodus*, which may represent gut contents. In addition, the holotype specimen of the large eogyrinid *Pholiderpeton scutigerum* Huxley (BRM NS.111.81) is associated with two scales of the crossopterygian *Megalichthys* which, to judge from their situation and eroded condition, are probably also derived from ingested prey (J. A. Clack, pers. comm.). Although *E. attheyi* was probably mainly piscivorous, it seems highly likely that it fed also upon other aquatic tetrapods; there is, however, no direct evidence for this. A. R. Milner (1980b) has suggested that eogyrinids may have been adapted for swimming and/or crawling among dense *Calamites* stands around lake margins.

Eogyrinids appear to be scarce in tetrapod assemblages from shallow-water/swamp-lake environments. Only two incomplete specimens of the, doubtfully eogyrinid, embolomere *Diplovertebron punctatum* Fritsch were reported by A. R. Milner (1980b) from Nýřany. Panchen (1977) noted only six specimens of *Leptophractus obsoletus* Cope from Linton. No precise published data are available concerning the frequency of eogyrinids in the Jarrow assemblage; however, Panchen (1970, p. 64) reported a mere two embolomere specimens from the site. Interestingly, the tetrapod assemblage from Joggins, which is composed mostly of terrestrial tetrapods (see below), includes a few specimens of the tiny, probably eogyrinid (Panchen 1970), embolomere *Calligenethlon watsoni* Steen. They are, however, relatively rare components of the assemblage (Carroll 1967) and, while the mode of their preservation suggests that they were capable of terrestrial locomotion, it is doubtful if larger eogyrinids were habitual overland travellers.

In summary, the relative frequency of *Megalocephalus*, *Batrachiderpeton*, and *Eogyrinus* specimens in the Newsham tetrapod assemblage, the nature of the material and the presumed mode of life of the animals themselves together suggest that these taxa were endemic in life to the environment of preservation. The scarcity of loxommatids, keraterpetontids, and eogyrinids in shallow-water/swamp-lake tetrapod assemblages would seem to confirm that the Westphalian members of these families were characteristic inhabitants of larger and deeper water bodies, such as the Newsham lake (text-fig. 4).

The structure of the Newsham open-water/lacustrine community has been discussed by A. R. Milner (1980b, pp. 475–479), who suggests that the ultimate energy sources in Carboniferous open-

water bodies such as the Newsham lake were probably organic detritus and algae, the former being fed upon by a wide range of invertebrate primary consumers and the algae, both planktonic and encrusting, mainly by ostracods and gastropods. Milner further suggests that all the endemic fish species at Newsham, with the possible exception of the platysomid palaeoniscid *Chirodus*, were, like the amphibians, secondary and tertiary consumers which fed upon other vertebrates and invertebrates. As noted elsewhere in the present paper, the only invertebrate taxa known from Newsham are ostracods and bivalves; the other invertebrate groups noted by Milner as possible carnivores (chelicerates) and primary consumers (palaeocarid crustaceans and gastropod molluscs) in open-water/lacustrine communities have not been reported from the site. However, all three are known from Westphalian non-marine deposits (e.g. Calver 1968; Schram 1976) and their absence from the Newsham assemblage may merely be due to non-preservation or non-collection. While generally in agreement with A. R. Milner's (1980b) conclusions with respect to the structure of the Newsham open-water/lacustrine community, the present writer would suggest that *Chirodus* (represented by a very few articulated specimens of *C. striatus* (Hancock and Atthey)) may not have been the only vertebrate primary consumer at the site. Two species of dipnoan, the ctenodontid *Ctenodus cristatus* Agassiz and the sagenodontid *Sagenodus inaequalis* Owen, have been reported from Newsham (S. M. Andrews *in Land* 1974, p. 61) and the latter, at least, may have been partly, if



TEXT-FIG. 5. Hypothetical food-web of the Newsham open-water/lacustrine community. The food-web is much simplified, for the sake of clarity, and does not attempt to show all possible interactions involving juveniles and larvae. Format based upon that employed by A. R. Milner (1980b, fig. 9).



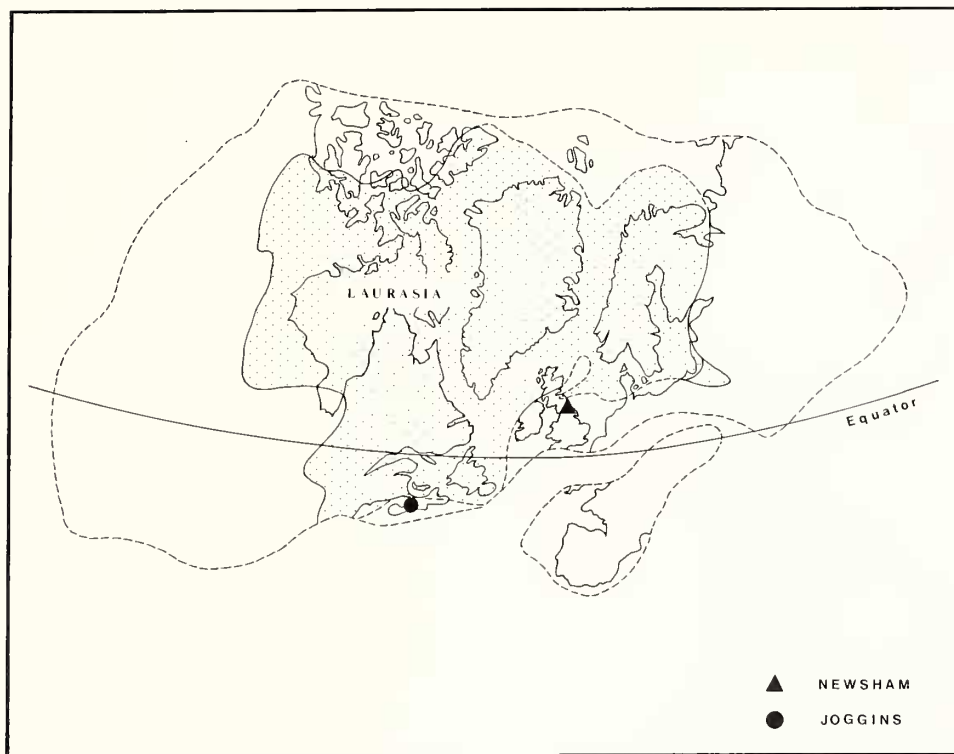
not entirely, herbivorous. Unlike the tooth-plates of *Ctenodus*, which appear to have been specialized for crushing, those of *Sagenodus* bear a reduced number of ridges and denticles and were probably mainly sectorial in function (Moy-Thomas and Miles 1971, p. 152). It is interesting to note, moreover, that both juveniles and adults of *Neoceratodus*, structurally the most primitive of the living Dipnoi, are known to take vegetable, as well as animal food. Indeed, Günther (1880, p. 357) noted that the stomach of *Neoceratodus* specimens usually contains large quantities of leaves derived from plants growing on river banks, which are evidently eaten after falling into the water. If one or both of the Newsham dipnoans included significant amounts of plant material in their diet, they must have been much more important as primary consumers than the, rare, *Chiroodus striatus*; a cursory survey of the extensive Newsham fish collections in the Hancock Museum suggests that the Dipnoi may be the most abundantly represented group. Moreover, Hancock and Atthey (1871*b*, p. 197) note that Atthey's collection at that date included at least 400 isolated dipnoan tooth-plates from Newsham, representing a minimum of 100 individuals. Like *Neoceratodus*, the juveniles of the Newsham lungfish may have eaten filamentous algae and the adults may have taken both living and dead vascular plant material, including, perhaps, *Calamites* growing around the lake margins.

Text-fig. 5 is a hypothetical food-web of the Newsham open-water/lacustrine community, which incorporates the above suggestions.

#### THE JOGGINS TETRAPOD ASSEMBLAGE

As noted above, only one other large, compact tetrapod assemblage of Westphalian B age is known, that from Joggins in Nova Scotia (text-fig. 6). All described tetrapod specimens from this site were collected from within Division 4 (*sensu* Logan 1845) of the lower Westphalian B Cumberland Group, on the south side of Chignecto Bay at the head of the Bay of Fundy (Carroll 1967). Division 4 of the Cumberland Group includes approximately forty horizons at which erect stumps of arborescent lycopods, including *Sigillaria*, occur. All but a very few of the Joggins tetrapods were found within these stumps. As Carroll (1967, p. 112) has pointed out, 'the preservation of the stumps in an erect position is apparently a result of very rapid deposition. In the cases where vertebrates are found within the trees, it is probable that the bases of the trees were covered but most of the trunk remained exposed. The portion of the trees remaining above the new ground level then fell over, and the centre of the stumps (pulpy even in the living trees) rotted out. The resulting hollow cylinders served as traps for animals living on the new land surface.' Rayner (1971, p. 463), however, has suggested that at least some of the Joggins tetrapods may have deliberately entered the hollow stumps in search of food. The Joggins assemblage has been briefly reviewed by Carroll *et al.* (1972, pp. 64-80).

Comparison of the tetrapod assemblages from Newsham and Joggins is of some interest in view of the fact that they are closely contemporaneous but preserved in sediments deposited in two very different micropalaeoenvironments within broadly similar (coal-swamp basin) macropalaeoenvironments. The fact that the Joggins lycopod stump tetrapods were collected from a number of different horizons within over 450 m of strata (Carroll *et al.* 1972), whereas the Newsham assemblage derives entirely from one bed of shale no more than 10 cm thick (Atthey 1877), is probably of less significance for such a comparison than initial consideration might suggest. The Newsham black shale was apparently laid down during a period of very low detrital input into (at least the centre of) the Newsham lake and sedimentation may have been very slow. Conversely, the presence at Joggins of erect lycopod stumps up to 9 m in height is, as noted by Carroll (1967) and Rayner (1971), indicative of very rapid sedimentation. The lengths of time represented by the tetrapod-bearing deposits at the two localities may thus not be so widely disparate as suggested by the differing thicknesses of strata involved. The ten valid tetrapod species so far recorded from the Joggins lycopod stumps are listed below. Where possible, data (derived from the literature) on the frequency of each species at the site have been included, as has an indication of size. The latter is, in most cases, given as skull length, as many of the Joggins tetrapods are known only from disarticulated and incomplete skeletons.



TEXT-FIG. 6. Map of Laurasia during mid-Carboniferous times to show approximate positions of Joggins and Newsham relative to one another and to the southern margin of the continent. Stippling indicates terrestrial hinterland; unstippled area of continent comprises shelf seas and marginal environments (map modified from Johnson 1981, fig. 4).

#### Order TEMNOSPONDYLI

Dendrerpetontidae: *Dendrerpeton acadianum* Owen—‘about 100 specimens’ (Carroll 1967, p. 111). The largest described skull of this species from Joggins has a midline length of 102 mm and, as restored by A. R. Milner (1980a, fig. 3D), a total length of about 120 mm.

#### Order BATRACHOSAURIA

Eogyrinidae: *Calligenethlon watsoni* Steen—‘less than a dozen specimens’ (Carroll 1967, p. 111). Carroll (1967) estimates the skull of this species to have been between 50 mm and 75 mm in length.

#### Order MICROSAURIA

Tuditanidae: *Asaphestera intermedia* (Dawson)—twenty identifiable specimens. The larger skulls have a total length of about 42 mm (Carroll and Gaskill 1978).

Pantylidae: *Trachystegos megalodon* Carroll—five identifiable specimens (Carroll and Gaskill 1978). The total length of the skull as restored by Carroll (1966, fig. 11B) is 53 mm.

Gymnarthridae: *Leiocephalikon problematicum* (Dawson)—ten identifiable specimens. The total length of the skull appears to have been about 21 mm (Carroll and Gaskill 1978).

Gymnarthridae: *Hylerpeton dawsoni* Owen—fourteen identifiable specimens (Carroll and Gaskill 1978). The total length of the skull is not known but the left mandibular ramus figured by Carroll (1966, fig. 6A) is 37 mm long.

Hapsidopareiontidae: *Ricnodon* sp.—four identifiable specimens (Carroll and Gaskill 1978). The total length of the skull is unknown but the isolated dentary figured by Carroll (1966, fig. 19B) measures about 9 mm in length.

#### Order CAPTORHINOMORPHA

Romeriidae: *Hylonomus lyelli* Dawson—eighteen specimens (Carroll *et al.* 1972). The skull of the type specimen is 33 mm in length (Carroll and Baird 1972).

Romeriidae: *Archerpeton anthracos*—sixteen specimens (Carroll *et al.* 1972). This species is known from very incomplete remains; it is, however, clearly substantially smaller than *Hylonomus* (Carroll and Baird 1972).

#### Order PELYCOSAURIA

?Ophiacodontidae: *Protoclepsydrops haplous* Carroll—four specimens (Reisz 1972). The skull is not known in its entirety but the humeral length of this species is only slightly less than that of the Westphalian D ophiacodont pelycosaur *Archaeothyris florensis* (Reisz 1972, fig. 18), which has a skull about 92 mm in length.

All the above listed species, with the possible exception of *Calligenethlon watsoni*, appear to have been largely terrestrial in habit (e.g. Carroll 1967; Carroll and Gaskill 1978; Carroll and Baird 1972; Reisz 1972) and are members of families regarded by A. R. Milner (1980*b*) as belonging to the Westphalian terrestrial/marginal tetrapod association. *C. watsoni* is, as noted above, the smallest described embolomere and may have been more terrestrial than other known eoogyrinids.

The Eogyrinidae, represented at Joggins by *C. watsoni*, is the only tetrapod family common to both this assemblage and that from Newsham. Microsaurs (*sensu* Carroll and Gaskill 1978), pelycosaur and captorhinomorph reptiles and dendrerpetontid temnospondyls have not been reported from Newsham. Loxommatids, keraterpetontid and urocordylid nectrideans, lysorophids, ophiderpetontid aïstopods and anthracosaurid embolomeres are not known from the Joggins erect stumps. The differences in the composition of the two assemblages clearly reflect their differing environments of preservation. Most, if not all, of the Joggins tetrapods were primarily terrestrial forms whereas the Newsham assemblage is composed almost entirely of amphibians which were either endemic to the lake in whose bottom sediments they were preserved or derived from other aquatic environments. However, a second difference exists between the tetrapod assemblages from the two sites. Whereas the Newsham assemblage includes both small and very large amphibian species, that from Joggins is composed only of relatively small tetrapods. The largest species reported from the erect stumps appears to be *Dendrerpeton acadianum*, with a recorded skull length of up to 120 mm. A. R. Milner (1980*a*, p. 126) has suggested that the known members of this genus probably grew to about one metre in total length. The absence of larger tetrapods at Joggins is, as suggested by Carroll *et al.* (1972, p. 71), probably due to the manner in which the assemblage was preserved; tetrapods above a certain size would have been unlikely to fall into the, 0.9m–1.2 m diameter, hollow lycopod stumps or, if they did so, may have been able to extricate themselves. The operation of this filter, controlling the size of the animals preserved, may explain the absence from the Joggins assemblage of the only terrestrial/marginal tetrapod species known from Newsham, the large anthracosaurid embolomere *Anthracosaurus russelli*, or any other representative of the Anthracosauridae.

Of the seven tetrapod families represented at Joggins but not at Newsham, all but one (Pantylidae) occur also in the Westphalian of Europe, either at Jarrow (Dendrerpetonidae: A. R. Milner 1980*a*) or at Nýfany (Tuditanidae, Gymnarthridae, Hapsidopareiontidae, Romeriidae, Ophiacodontidae: A. R. Milner 1980*b*, p. 453). Similarly, all but one (Anthracosauridae) of the six families occurring at Newsham, but not Joggins, are present in the North American Westphalian at Linton, Ohio (Loxommatidae, Keraterpetontidae, Urocordylidae, Lysorophidae, Ophiderpetontidae: Romer 1930). It thus seems likely that the constitutional differences between the tetrapod assemblages from Joggins and Newsham are largely, if not entirely, due to the differing coal-swamp basin micropalaeoenvironments represented by the tetrapod-bearing deposits at the two sites. The writer



would, therefore, suggest that the two assemblages may be regarded as complementary, and as together providing a more balanced and complete picture of the Westphalian B lowland tetrapod fauna of southern Laurasia than either does alone.

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*Note added in proof.* Since the present paper went to press, preparation of a hitherto enigmatic specimen (Hancock Museum, no. G.2484) from Newsham has enabled it to be identified as the skull table of a romeriid reptile. This new reptile forms an addition to the terrestrial/marginal tetrapod assemblage. A full description of the material will shortly be published.